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Global divergent responses of primary productivity to water, energy, and CO<sub>2</sub>

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## Abstract

The directionality of the response of gross primary productivity (GPP) to climate has been shown to vary across the globe. This effect has been hypothesized to be the result of the interaction between multiple bioclimatic factors, including environmental energy (i.e. temperature and radiation) and water availability. This is due to the tight coupling between water and carbon cycling in plants and the fact that temperature often drives plant water demand. Using GPP data extracted from 188 sites of FLUXNET2015 and observation-driven terrestrial biosphere models (TBMs), we disentangled the confounding effects of temperature, precipitation and carbon dioxide on GPP, and examined their long-term effects on productivity across the globe. Based on the FLUXNET2015 data, we observed a decline in the positive effect of temperature on GPP, while the positive effects of precipitation and CO<sub>2</sub> were becoming stronger during 2000–2014. Using data derived from TBMs between 1980 and 2010 we found similar effects globally. The modeled data allowed us to investigate these effects more thoroughly over space and time. In arid regions, the modeled response to precipitation increased since 1950, approximately 30 years earlier than in humid regions. We further observed the negative effects of summer temperature on GPP in arid regions, suggesting greater aridity stress on productivity under global warming. Our results imply that aridity stress, triggered by rising temperatures, has reduced the positive influence of temperature on GPP, while increased precipitation and elevated CO<sub>2</sub> may alleviate negative aridity impacts.

## Introduction

Terrestrial gross primary productivity (GPP), the total carbon uptake by photosynthesis of plants per ground

area at the ecosystem scale, is the largest component of the global carbon cycle (Beer *et al* 2010) and helps to offset anthropogenic emissions of CO<sub>2</sub> (Battin *et al* 2009). GPP provides the energy that drives other

biological activities, and its changes, in either magnitude or direction, could profoundly affect regional and global hydrological and biogeochemical cycles (Poulter *et al* 2014, Ma *et al* 2015). In recent decades, global climate change has greatly altered GPP across different geographic regions (Zhang *et al* 2009, Garbulsky *et al* 2010, Anav *et al* 2015, Burley *et al* 2016, Hao *et al* 2018). Therefore, understanding spatiotemporal changes in the responses of GPP to climatic forcing is important for making reliable projections of future biosphere-atmosphere feedbacks.

To date, many studies have shown that year-to-year variability of GPP is largely driven by the variations of energy- and water-related climate variables, including temperature, solar radiation, precipitation as well as CO<sub>2</sub> (Nemani *et al* 2003). The directionality of the changes in GPP in response to these climate variables can be both positive and negative across different regions and periods. For example, increasing temperatures under global warming have been shown to increase GPP worldwide (Luo 2007, Anav *et al* 2015). However, due to rising temperatures, water stress could occur by increasing evaporative demand that cannot be met by soil water supply (Sperry 2000). Correspondingly, declining trends in GPP with increasing temperature have been widely reported, including in both temperate and tropical forests (Ciais *et al* 2005, Saleska *et al* 2007). Contrasting responses of primary productivity to changes in precipitation are also observed in grasslands (Heisler-White *et al* 2008, Wu *et al* 2018) and tropical forests (Taylor *et al* 2017). The interactive effects of water and energy further complicate the predictions of the spatio-temporal changes in their effects on the GPP under global warming (Zhao and Running 2010). A global analysis is therefore imperative to clarify the responses of the GPP to climate drivers in order to reconcile observed contradictory relationships, and to more accurately predict the impacts of global climate change on carbon cycling.

Eddy covariance (EC) flux towers provide an accurate way to measure and calculate the carbon flux and GPP (Baldocchi *et al* 2001). However, flux measurements are usually constrained by relatively small spatial and temporal scales (Baldocchi *et al* 2001, Falge *et al* 2002). In contrast, observation-driven terrestrial biosphere models (TBMs) can simulate long-term temporal changes in GPP over large spatial scales, which have been used in the Multi-scale synthesis and Terrestrial Model Intercomparison Project (MsTMIP) (Huntzinger *et al* 2013, Zscheischler *et al* 2014, Mao *et al* 2015, Schwalm *et al* 2017). However, the accuracy of the modeled GPP cannot be guaranteed because it is difficult for terrestrial ecosystem models to simulate the complicated effects of a series of climatic factors (e.g. water and energy) on GPP in natural ecosystems (Smith *et al* 2016). Previous studies have demonstrated a discrepancy between the GPP modeled by TBMs and measured by field experiments (Smith *et al* 2016,

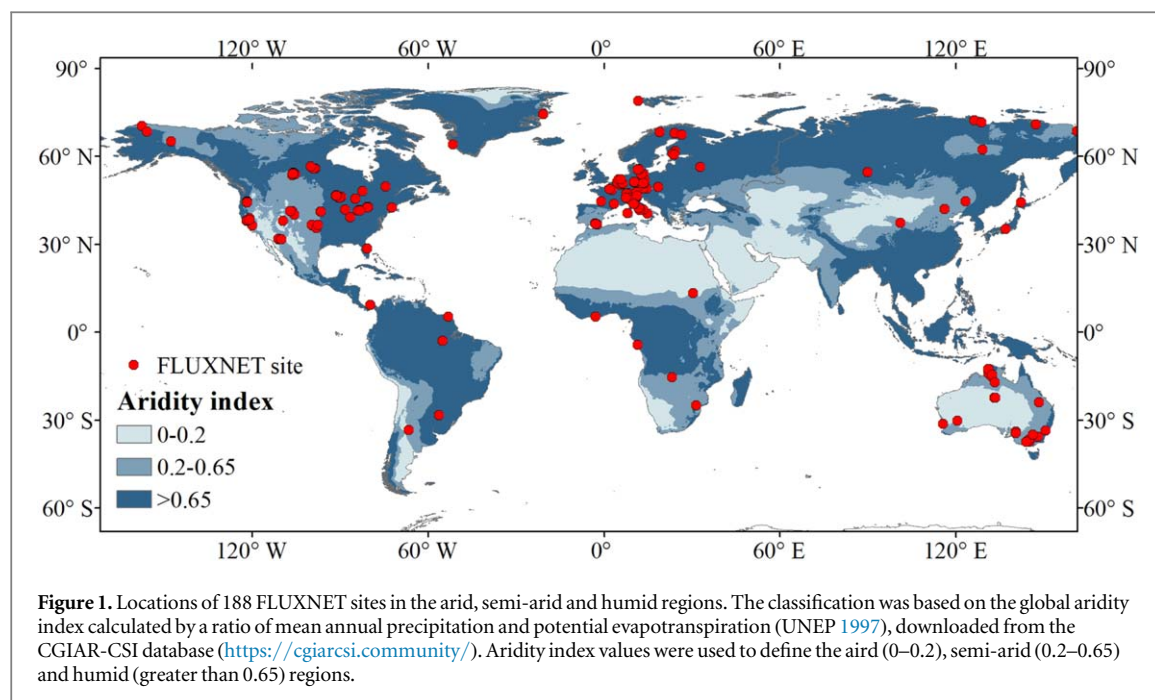
Kolus *et al* 2019, Winkler *et al* 2019). EC-derived GPP can be used to validate the accuracy of the TBMs regardless of the constrained scales over time and space. It is therefore important to combine the GPP data based on flux towers and TBMs to study the complicated effects of climatic drivers on GPP under global warming.

Combining the GPP data from flux network (FLUXNET2015) and TBM models, herein we aimed to examine (1) whether the effects of temperature, precipitation and CO<sub>2</sub> on GPP vary over time, especially in recent decades under the global warming, and (2) whether the long-term responses of GPP to water and energy in arid and humid regions are consistent or not. Unlike existing studies, we disentangled the confounding effects of water, energy, and CO<sub>2</sub> and investigated their long-term effects on GPP at the global scale between 1901 and 2010. To this end, we first quantified the year-to-year effects of temperature, precipitation, and CO<sub>2</sub> on GPP for arid regions, semi-arid regions, and the entire globe over the past century. Subsequently, we attempted to detect the changing point of the climate-GPP relationship at the regional and global scale by combining nonlinear and linear models. We hypothesized that the relative influence of water has increased in recent decades due to potential aridity stress triggered by climate warming.

## Materials and methods

### GPP and climate data

The modeled GPP data are obtained from MsTMIP Global Simulation which is a formal synthesis activity including a community of different land carbon models (<https://nacp.ornl.gov/mstmipdata/>). This project is a formal model intercomparison and evaluation effort aimed at improving the diagnosis and attribution of carbon exchange at local and global scales (Huntzinger *et al* 2013). The MsTMIP simulations were performed using a standardized simulation protocol and were all forced using the same climate drivers, including standard weather drivers, remotely sensed phenology, biome classification, land-use history, and disturbance. The variations in model structure include varying processes types (e.g. nutrient cycling, disturbance, lateral transport of carbon), and how these processes are represented (e.g. photosynthetic formulation, temperature sensitivity, respiration) in the models. More detailed information about the MsTMIP was described in some existing studies (Huntzinger *et al* 2013, Wei *et al* 2014). The MsTMIP provides monthly simulation results across the globe (spatial resolution: 0.5° × 0.5°) from 1901 to 2010. By following Schwalm *et al* (2017), an ensemble GPP mean are derived from the MsTMIP Version 1 models (CLM, CLM4VIC, DLEM, ISAM and TEM6) including all time-varying factors (BG1). These simulations used include the identical time-varying climate and



atmospheric CO<sub>2</sub> concentrations, land use and land cover change, and nitrogen deposition. The MsTMIP simulations has been widely used in many existing studies (Zscheischler *et al* 2014, Mao *et al* 2015, Schwalm *et al* 2017).

Also, we used the observed GPP data and associated climate data from the FLUXNET gauge observations (<https://fluxnet.fluxdata.org/data/>). The FLUXNET is a uniform and high-quality dataset based on regional flux networks worldwide. The latest release of the FLUXNET data (FLUXNET2015) was used in this study, which includes over 1500 site-years of data from 212 sites (<http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>). Since very limited data are available before 2000 regarding the FLUXNET2015 dataset, we constrained our observation-based analysis to the period 2000–2014 using sites with available GPP and climate data, including temperature, precipitation, radiation and CO<sub>2</sub> (188 sites in total, 159 sites in Northern Hemisphere and 29 sites in Southern Hemisphere) (see figure 1).

Gridded monthly mean temperature and precipitation were obtained from the Climate Research Unit (CRU) TS3.25 climate dataset (<http://cru.uea.ac.uk/cru/data/hrg/>). The gridded monthly mean radiation data were generated by simple process-led algorithms for simulating habitats (SPLASH version 1.0) based on CRU cloud cover data (Davis *et al* 2017). The climate gridded data span the period 1901–2010 with a spatial resolution of 0.5°.

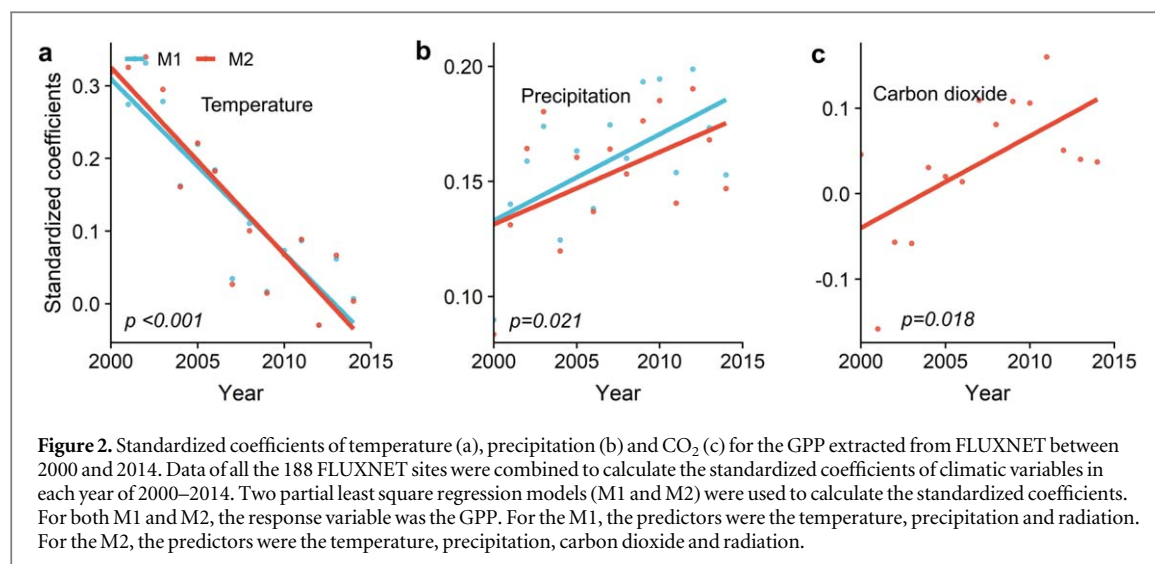
To investigate and compare the effects of climate variables on GPP in arid and humid regions during 1901–2010, we also classified the global surface into arid, semi-arid and humid regions (see figure 1) based on the global-aridity index calculated by a ratio of mean annual precipitation and potential

evapotranspiration (UNEP 1997). The global aridity index was downloaded from the CGIAR-CSI database (Zomer *et al* 2008) (<https://cgiarcsi.community/data/global-aridity-and-pet-database/>).

### Climate-GPP relationship

Partial least square regression (PLSR) was used to quantify the effect of monthly temperature, precipitation, radiation and CO<sub>2</sub> on modeled and measured GPP across the globe by taking into account the potential multicollinearity between factors (Hoerl and Kennard 1970, Graham 2003). Using the FLUXNET data, we analyzed the effects of temperature, precipitation, CO<sub>2</sub> on measured GPP between 2000 and 2014. In the PLSR model, the response variable was GPP and the predictors were CO<sub>2</sub>, temperature, precipitation and short-wave radiation in each year of 2000–2014. All the sites were combined for each year when analyzing the effects of climatic drivers on GPP. Note that radiation was incorporated into each model as a covariate to exclude its effect on GPP. Both the response variables and predictors were standardized in the model. The standardized regression coefficients (Schielzeth 2010) were calculated using the PLSR models to compare the extent of influence of climatic variables on GPP. Linear regression models were used to quantify the temporal trends in standardized regression coefficients of CO<sub>2</sub>, temperature, precipitation on GPP between 2000 and 2014.

Unlike gridded temperature and precipitation data, similar CO<sub>2</sub> data between 1901 and 2010 were not available. Therefore, we only examined the effects of monthly mean temperature and precipitation on GPP between 1901 and 2010 simulated by the MsTMIP. To compare the responses of GPP to climatic drivers, we conducted separate analyses for arid



regions, semi-arid regions, and the entire globe. The response variable was monthly GPP and the predictors were monthly temperature, precipitation, and radiation for each year. For each year of 1901–2010, all the pixels in arid, semi-arid, and humid regions were combined to calculate the standardized regression coefficients. To test the consistency between FLUXNET and the MsTMIP, we also examined the effects of temperature and precipitation alone on FLUXNET2015 GPP between 2000 and 2014. We standardized the response and predictor variables to calculate the standardized coefficients of PLSR models. The monthly calculated standardized coefficients in each year were averaged to represent the annual effect of climatic variables on GPP to compare with the results of FLUXNET. Local polynomial regressions were used to smooth and identify the changing points of the time series of standardized coefficients in arid, semi-arid regions and across the globe. Linear regression models were subsequently used to test the statistical significance of the temporal trends in standardized coefficients. Local polynomial regressions and linear regression models were also used to analyze the trends of the annual mean temperature, precipitation in arid regions, semi-arid regions, and the entire globe between 1901 and 2010. All of the data analyses were conducted using R version 3.5.1 (R Core Team 2018).

## Results

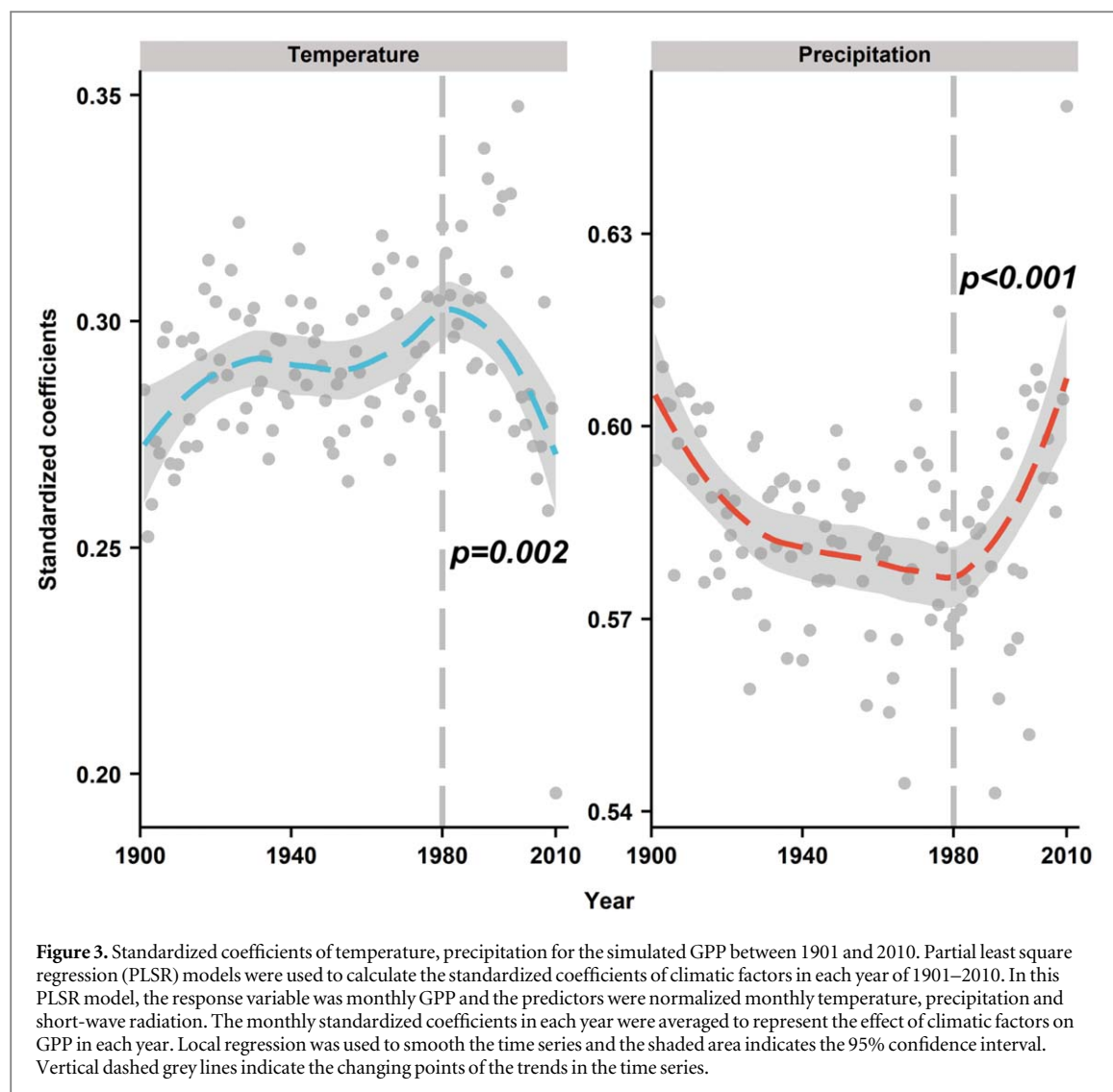
On the basis of FLUXNET2015 data, when not considering CO<sub>2</sub>, we found that the positive effect of temperature on GPP showed a significant decrease between 2000 and 2014 across the globe (figure 2). However, we observed a significant increase in the positive influence of precipitation over that time period at the global scale (figure 2). When incorporating CO<sub>2</sub> into the PLSR models, the positive effect of temperature and precipitation also showed declining and increasing trends, respectively (figure 2). As with

precipitation, the effect of CO<sub>2</sub> on GPP also showed a significant increase during 2000–2014 across the globe (figure 2). On the basis of MsTMIP simulations, between 1901 and 1980, the overall positive effect of temperature on GPP showed an increasing trend (figure 3). In contrast, a decreasing trend in the positive effect of precipitation on GPP was observed before 1980 (figure 3). At the global scale, between 1980 and 2010, the positive effect of temperature on GPP showed a significant decrease at the global scale, whereas a significant increase in the positive effect of precipitation was observed since 1980 (figure 3).

The temporal changes in the effect of annual temperature and precipitation on GPP in arid, semi-arid, and humid regions between 1901 and 2010 is shown in figure 4. In arid and semi-arid regions, the positive effect of annual precipitation on GPP increased over time since 1950. In humid regions, we also observed a significant increase in the positive effect of annual precipitation, but this did not begin until 1980, later than that in arid and semi-arid regions. In arid regions, the negative effect of annual temperature on GPP was reduced during the entire period 1901–2010. In semi-arid regions, the positive effect of annual temperature on GPP increased during 1901–1950. The positive effect of annual temperature on GPP in humid regions also increased before it started to decline. However, the increasing trend lasted until 1980 in humid regions, approximately 30 years later than semi-arid regions. Between 1950 and 2010, the positive effect of annual temperature remained stable in semi-arid regions. However, a decreasing trend in the positive effect of temperature on GPP since 1980 in the humid region was observed (figure 4).

Between 1980 and 2010, the positive effect of monthly precipitation was stronger than that of temperature on GPP across the globe (figure 5). In addition, the magnitude in the positive effect of monthly temperature on GPP was significantly lower in warm





months compared with cold months across the globe, becoming negative in summer months in arid and semi-arid regions (figure 5). In contrast, the extent of the positive influences of monthly temperature and precipitation in warm months was similar in humid regions (figure 5).

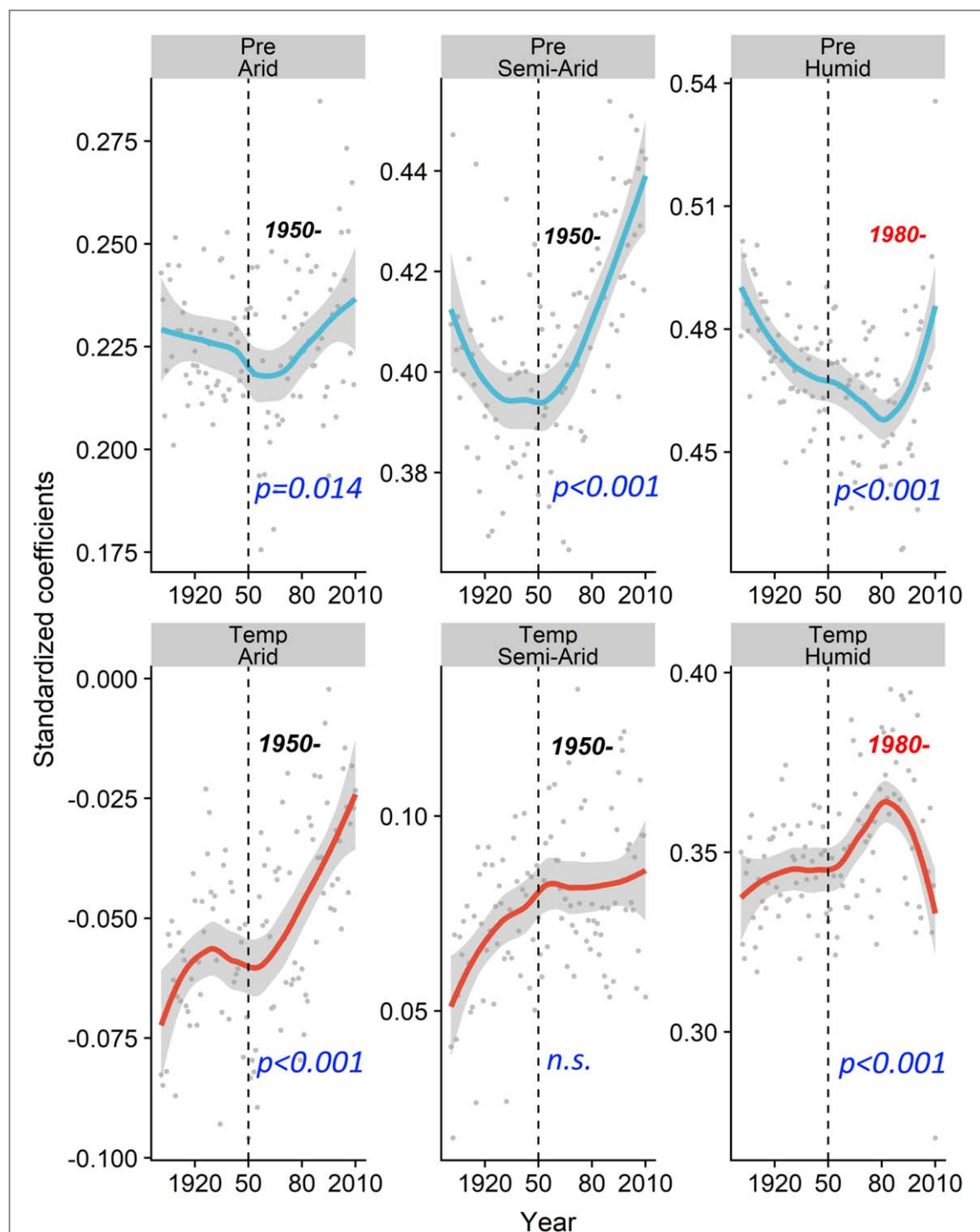
Between 1980 and 2010, annual mean temperatures showed significant increases in all regions (figure 6). Except for semi-arid regions, significant increasing trends in monthly total precipitation were also observed since 1980 (figure 6). It is noteworthy that the increasing rate of temperature was significantly faster than that of precipitation as indicated by the steeper slopes (figure 6).

## Discussion

Using comprehensive statistical analysis, we disentangled the confounding effects of water and energy, CO<sub>2</sub> and quantified their long-term effects on GPP at the global scale between 1901 and 2010. We found a decreasing effect of temperature on GPP across the globe since 1980 (figures 2 and 3). On the contrary, the

effect of precipitation on GPP showed a significant increase all over the globe (figures 2 and 3). These results reveal that water availability is becoming an increasingly limiting factor affecting global primary productivity in recent decades under global warming. Since 1980, temperatures have been increasing globally to a greater degree than precipitation (figure 6). The extra heat may increase evaporative demand and trigger drought events under global warming (Dai 2013, Trenberth *et al* 2014).

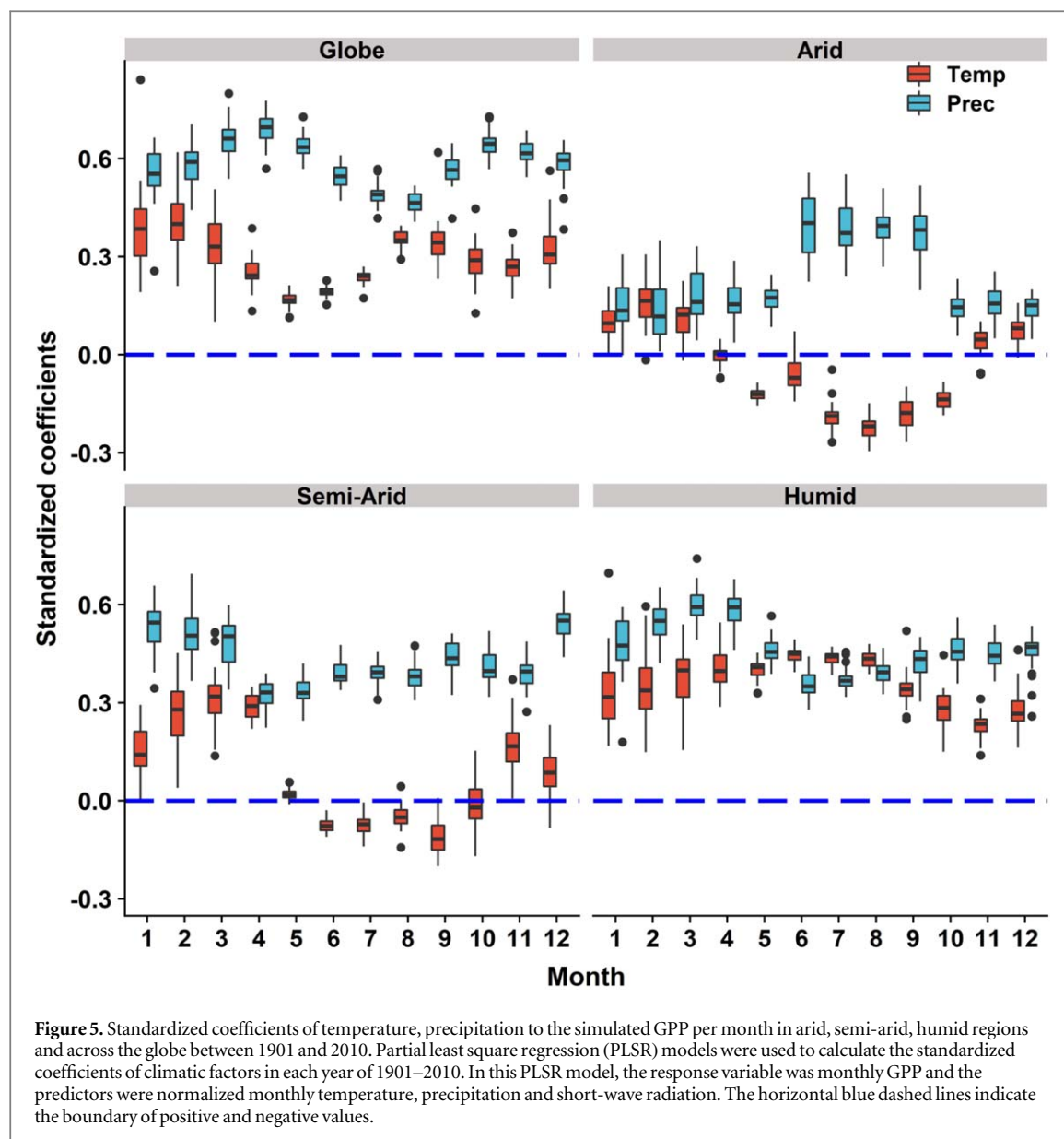
Generally, GPP shows a positive trend with rising surface temperature due to the enhanced photosynthesis (Luo 2007, Anav *et al* 2015). However, reduced primary productivity caused by severe drought events triggered by climate warming has also been widely reported (Ciais *et al* 2005, Allen *et al* 2010, Trenberth *et al* 2014, Chen *et al* 2017). For instance, in regional to subcontinental scale, studies documented that extensive droughts have dominantly contributed to the reduction in productivity in the China's terrestrial ecosystems between 2000 and 2011 (Liu *et al* 2014). The functional responses of production are quite sensitive to annual precipitation in North American



**Figure 4.** Standardized coefficients of temperature, precipitation to the simulated GPP in arid, semi-arid and humid regions between 1901 and 2010. Partial least square regression (PLSR) models were used to calculate the standardized coefficients of climatic factors in each year of 1901–2010. In this PLSR model, the response variable was monthly GPP and the predictors were normalized monthly temperature, precipitation and short-wave radiation. The monthly standardized coefficients in each year were averaged to represent the effect of climatic factors on GPP in each year. Local regression was used to smooth the time series and the shaded area indicates the 95% confidence interval. Vertical dashed grey lines indicate the changing points of the trends of the time series in arid and semi-arid regions. Linear regression was used to test the significance of the trends ( $p < 0.05$ ), and n.s. represent not significant ( $p > 0.05$ ).

grassland ecosystems (Knapp and Smith 2001, Suttle *et al* 2007). Moran *et al* (2014) reported that drought-induced grass mortality has resulted in shifts in the functional response to annual total precipitation in the desert grasslands of southwestern United States. In Western Atlantic regions and Eastern Europe, the precipitation deficits are strongly related to the decreased

productivity (Ivits *et al* 2014). In addition, existing studies have documented that the terrestrial primary productivity is largely driven by the droughts events in Australia (Donohue *et al* 2009, Ma *et al* 2015). The reduced primary productivity by drought events may counteract and reduce the beneficial effect of temperature on primary productivity. Due to the drought



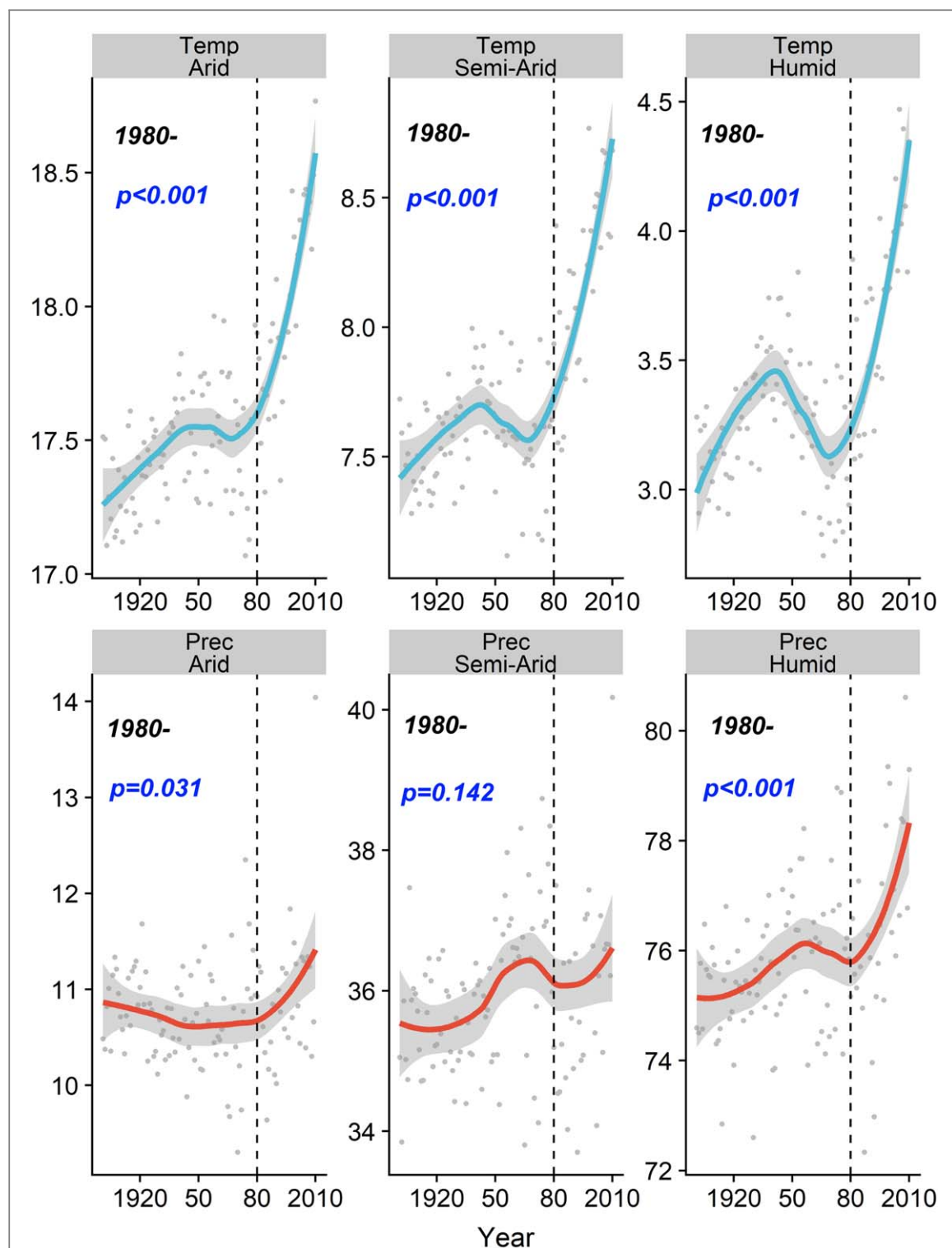
stress, water availability would therefore become increasingly important for global primary productivity. As such, the GPP showed declining and increasing responses to temperature and precipitation since 1980, respectively.

Plants are more likely to suffer water stress in arid regions than in humid regions due to the greater heat and higher evaporative demand coupled with less soil water availability, particularly in warm seasons (Zou *et al* 2005, Liu *et al* 2013, Tomlinson *et al* 2013). Consistently, we observed negative effects of summer temperature on the GPP in arid regions, but it was positive in humid regions (figure 5). These regional differences of water and heat conditions presented above well explain why the positive effect of precipitation on the GPP increased earlier (approximately 20 years) in arid regions than in humid regions (figure 4). In addition, we observed a reduced negative effect of temperature in arid regions since 1950 (figure 4). Similarly, the positive effect of annual precipitation also

showed a significant increase in arid regions in the past decades (figure 4). However, the positive effect of temperature on GPP did not increase with the increasing precipitations in semi-arid and humid regions (figure 4). These findings suggest that the increased water is able to mitigate the effect of water stress on GPP in arid regions, but not in humid regions. This could be contributed by the fact that plants hold more plastic and rapid responsive strategies, such as smaller leaf size, higher leaf phosphorous content (Tomlinson *et al* 2013) and longer root systems (Orians and Solbrig 1977), to changing water availability in arid regions compared with those in humid regions (Vicente-Serrano *et al* 2013).

Using Free-Air Carbon dioxide Enrichment experiments, many studies have shown that increasing atmospheric CO<sub>2</sub> can effectively increase productivity by increasing photosynthetic rates (Nowak *et al* 2004). Furthermore, the response of plant growth to increasing CO<sub>2</sub> is often amplified under water-stress





**Figure 6.** Mean monthly temperature (°C) and precipitation (mm) in arid, semi-arid and humid regions between 1901 and 2010. Partial least square regression (PLSR) models were used to calculate the standardized coefficients of climatic factors in each year of 1901–2010. In this PLSR model, the response variable was monthly GPP and the predictors were normalized monthly temperature, precipitation and short-wave radiation. The monthly standardized coefficients in each year were averaged to represent the effect of climatic factors on GPP in each year. Local regression was used to smooth the time series and the shaded area indicates the 95% confidence interval. Vertical dashed grey lines indicate the changing points of the trends in the time series. Linear regression was used to test the significance of the trends ( $p < 0.05$ ), and n.s. represent not significant ( $p > 0.05$ ).

conditions (Field *et al* 1997, Morgan *et al* 2004). Therefore, the observed increase in the positive influence of CO<sub>2</sub> on GPP across the globe since 2000 (figure 2) is possibly due to a CO<sub>2</sub>-induced alleviation of water stress.

It is important to point out the shortcomings of our study that future research should address. First, whether the effects of water availability on ecosystem respiration also increases in recent decades deserves further examination. Second, productivity is also co-

limited by other factors in addition to water, energy and CO<sub>2</sub>, such as soil nutrient (e.g. nitrogen) (Reich *et al* 2014, Terrer *et al* 2018) and leaf area index (Gitelson *et al* 2014, Croft *et al* 2015). The factors affecting productivity have not yet been addressed fully.

Taken altogether, our study provides evidence that since 1980 GPP is becoming more strongly regulated by water availability at the global scale. On the contrary, the positive effect of increasing temperature on GPP has started to decline since 1980. The contrasting responses of GPP to water and energy may be due to the negative impact of aridity stress triggered by the increase of evaporative demand under global warming.

## Conclusions

Existing studies have widely shown that GPP is influenced by environmental energy and water availability. However, the influences of energy and water on productivity are not only mixed but also contrasting across different regions. Using PLSR models, we uncoupled their confounding effects and investigated the spatiotemporal changes in the climate-productivity relationship over the past century. By combining the GPP extracted from the FLUXNET and simulated by the MsTMIP, we observed a decreasing trend in the effect of temperature on GPP since 1980. However, the effect of precipitation and CO<sub>2</sub> on the GPP showed significant increases. Our results imply that water availability is becoming increasingly important to the global GPP due to the rise in the evaporative demand as global warming continues. The negative impact of water stress fractionally offset the warming-induced increase in GPP. This contributed to a decline in the positive effect of temperature on GPP in recent decades. Currently, the GPP still generally increases with temperature at the global scale. However, aridity is projected to become more frequent and widespread at the global scale under future climate scenarios (Sheffield and Wood 2008, Dai 2013). Therefore, the observed decreasing trends in the positive effect of temperature on GPP might continue in the coming decades.

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## Data availability

The data that support the findings of this study are openly available: MsTMIP (<https://nacp.ornl.gov/mstmipdata/>; <https://doi.org/10.3334/ORNLDAAC/1225>), FLUXNET (<https://fluxnet.fluxdata.org/data/>; data DOI is in preparation as stated by the data provider), CRU (<https://crudata.uea.ac.uk/cru/data/hrg/>; <http://doi.org/10.1002/joc.3711>), and Global aridity index (<https://cgiasi.community/data/global-aridity-and-pet-database/>; <https://doi.org/10.6084/m9.figshare.7504448.v3>).

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